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EXPERIMENTAL ARTICLES

Spatial Peculiarities in the Colonization of the Plant Rhizoplane by Microscopic Fungi

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Abstract—Spatial peculiarities in the colonization of the tomato, cucumber, and barley rhizoplanes by microscopic fungi were studied. The apical zone of roots was colonized with a limited number of *R* strategists (the order *Mucorales*, *Fusarium* sp., *Aspergillus niger*, and *Mycelia sterilia*). The fungal population of the root hairs and the basal zone of roots was 2- to 3-fold denser due to the prevalence of *K* strategists. Fusaria, *Fusarium oxysporum* in particular, colonized roots in earlier terms than the genera *Trichoderma*, *Penicillium*, *Gliocladium*, and others. The *F. oxysporum* population was at a maximum in the rhizoplane zone nearest the root tip.

Key words: microscopic fungi, rhizoplane.

Some microscopic fungi have shown considerable promise for root pathogen control, which calls for knowledge of the regularities of their colonization, development, and spatial distribution in the plant rhizoplane. The relevant data concern mainly the above ground parts of plants [1, 2], whereas little is known about the primary colonization of the root system of plants and the invasion of plant tissues by fungal phytopathogens. The infection of roots by phytopathogenic fungi, such as *Pythium* and *Phytophthora*, occurs primarily in zones with maximum exudation of nutrients by the roots [2]. If plant seedlings are placed in a suspension of fungal zoospores, the latter, as a rule, accumulate in the zones of the root damage or elongation [3]. The zoospores of *Plasmodiophora brassicae* Wor., the causative fungus of the clubroot of crucifers, invade host plants through root hairs and the youngest epidermal cells. Presumably, fusaria infect plants in a similar way [1, 4, 5]. An important aspect of this problem is the reliable detection of the saprotrophic micromycetes that live in the zone of the phytopathogen invasion of roots.

The present work was undertaken to study the peculiarities of the colonization of plant roots by saprotrophic microscopic fungi.

MATERIALS AND METHODS

Experiments were carried out with the fusariosis-susceptible tomato hybrid F1, the cucumber cv. Crystal hybrid 116, and the barley hybrids 19034 and 18505.

Tomato and cucumber plants were grown in light soddy podzolic loamy soil of a hotbed at the Research Institute of Selection of Vegetable Crops (Mytishchi city, the Moscow region). Under laboratory conditions, tomato and cucumber plants were grown in the same soil for 3 weeks.

Barley plants were grown for 2 weeks in heavy soddy podzolic loamy soil taken from the top soil horizon (0–20 cm in depth) on the territory of the Soil Ecology Station of Moscow State University (Chashnikovo, the Moscow region). The soil was preliminarily sieved through a 1-mm-mesh-size screen.

Unlike other researchers dealing with plant rhizoplane, we did not wash roots but carefully cleaned them by removing the attached soil particles with sterile tweezers, a needle, and a brush. Such cleaning procedure is easy to perform when tomato and cucumber plants are grown in a well-structured hotbed soil with a high content of organic matter but is hardly appropriate for barley plants grown in a heavy loamy soil. For this reason, barley seeds were germinated in the soil between two layers of 150- to 250-μm-mesh-size nylon gauze, so that the barley seedling roots remained clean during the plant growth [6]. Such an approach did not noticeably affect the qualitative and quantitative composition of rhizoplane microorganisms: the populations of rhizoplane bacteria, actinomycetes, and fungi detected in the experiments with and without nylon gauze were found to be very similar, and the Sörensen similarity coefficients of the rhizoplane micromycete complexes detected in these two types of experiments were found to be higher than 80% [6].

Under laboratory conditions, plants were grown at room temperature under natural illumination in glass containers with a removable side wall. The container bottom was covered with a 1-cm layer of quartz sand overlaid with a 15-cm soil layer. Before sowing, the soil was wetted to 60–70% of the field moisture capacity

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Table 1. The mean radial growth rate of microscopic fungi in soddy podzolic soil and the rhizoplane of 1-week-old barley plants

Inoculation with	Medium	Mean radial growth rate, mm/h	
		soil	rhizoplane
Soil suspension dilutions and washings from roots and seeds	1*	0.08	0.14
	2**	0.07	0.13
Soil particles, seeds, and root fragments	1	0.41	0.44*
			0.55**
			0.49
	2	0.32	0.37*
			0.39**
			0.38

Note: 1, Czapek agar; and 2, Hutchinson agar.

* The rhizoplane of the barley hybrid 19304. ** The rhizoplane of the barley hybrid 18505.

through glass tubes penetrating the sand layer. The rhizoplane was sampled as follows. After removing the container's side wall, the roots appearing between the nylon gauze layers were carefully detached from the gauze and placed between sterile paper sheets for analysis (alternatively, small roots were placed in sterile petri dishes). Each root was divided into 8 regions: regions 1 and 2 corresponded to the zone of root sheath and elongation; regions 3–5 corresponded to the zone of root hairs; and regions 6–8 corresponded to the basal part of the roots. Each root was cut into pieces (fragments) 0.5–1 mm in length. Ten fragments from each of the eight root regions were placed on Czapek agar containing lactic acid or streptomycin for the analysis of their microbial population.

The abundance of a particular species in a given root zone was calculated as the ratio of the number of the root fragments of this root zone colonized by this species to the total number of the analyzed root fragments of this root zone. As a rule, one root fragment 0.5–1 mm in size gave rise to one fungal colony; i.e., under these analysis conditions, the species abundance (the number of micromycetes of a given species to the total number of detected fungi) corresponded to the occurrence rate of this species.

To detect fungi in the internal root tissues of withered plants, the root fragments were sterilized in 0.1% mercuric chloride for 1 min, ground in a mortar with a rubber-coated pestle, suspended in 10 ml of sterile water, and inoculated on the surface of Czapek agar. In comparative experiments with barley plants, both the root washings and the root fragments were inoculated on the surface of Czapek and Hutchinson agars. The mean radial growth rate was determined from the results of the 50–100 measurements of fungal growth in the soil and in the different rhizoplane zones. The colonies grown on agar media were counted at 5- to 20-h intervals [7, 8].

Microscopic fungi were identified by analyzing the relevant cultural and morphological characteristics [9–11].

Experiments with plants were carried out in 5 to 10 replicates. The results were statistically processed using the Statistica software program.

RESULTS

The mean radial growth rate of micromycetes in the rhizoplane of 1-week-old barley plants was considerably higher than that of soil micromycetes (Table 1) and was at a maximum (0.7–1.2 mm/h) in the zone of root elongation and root hair growth, as well as in the upper region of the basal part of the roots and on the surface of germinated seeds. The mean radial growth rates were found to be considerably higher when test agar media were inoculated with the melkozem (fine soil) particles, root fragments, and pieces of the outer cover of germinated seeds than when inoculated with the root washings or the soil suspension dilutions. As a result, 40–100% of fungal colonies became visible on the agar surface as early as 12 and 20 h after the agar inoculation with the root fragments and melkozem particles, against 23 and 43 h after agar inoculation with the root washings and the soil suspension dilutions. These data suggest that the first approach (inoculation with the root fragments and melkozem) makes it possible to reveal the active form of micromycetes (their mycelium rather than spores). Therefore, this approach is more appropriate to the investigation of the colonization of the plant rhizoplane by micromycetes.

Analysis showed that the typical fungi of tomato, cucumber, and barley rhizoplanes are the order *Mucorales*, *Fusarium oxysporum, F. solani, Alternaria alternata, Gliocladium catenulatum, Aspergillus niger, Penicillium purpurogenum, P. variabile, P. roquefortii, Verticillium lateritium, Trichoderma harzianum, T. koningii, Chaetomium* sp., and *Mycelia sterilia* (the families *Dematiaceae* and *Mucedinaceae*). A comparison of the cucumber and tomato rhizoplanes showed that the latter was more abundantly populated with *F. oxysporum, F. solani, Cladosporium cladosporioides, A. alternata, Acremonium* sp., and *Penicillium* spp. of the section *Biverticillata* and less abundantly populated with *G. catenulatum, Ulocladium botrytis, Fusarium sambucinum*, and *Mycelia sterilia*. The fungus *F. oxysporum* was also detected in the internal root tissues of the infected tomato and cucumber plants.

The rhizoplane of 1- to 2-week-old barley plants was the most abundantly populated with the order *Mucorales*, the genera *Fusarium, Penicillium, Alternaria, Trichoderma, Acremonium*, and *Zygorhynchus*, the species *Aspergillus niger*, and the family *Piptocephalidaceae*. The genera *Fusarium, Stysanus, Scopulariopsis*, and *Humicola* were less abundant in the rhizoplane of the barley hybrid 18505 than in the rhizoplane of the

Table 2. The spatial distribution of microscopic fungi over the roots of 2-week-old tomato plants

Fungal taxon	Fungal abundance, %							
	basal root zone		middle root zone				apical root zone	
	8	7	6	5	4	3	2	1*
Alternaria alternata			10					
Aspergillus fumigatus						10		
A. niger						10	10	
Chaetomium sp.					10			
Cladosporium herbarum		10	10					
Fusarium oxysporum			10		20	10	30	25
F. moniliforme	17						10	
F. solani				9				
Fusarium nivale	8							
Order *Mucorales*	25	20		18	20	10	40	50
Paecilomyces sp.				9				
Penicillium decumbens				9	10	10		
P. funiculosum		10	10					
P. purpurogenum	17	10		9				
P. variabile			10					
Penicillium sp.		10		9				
Trichoderma hamatum	17	30	20	27	20	30		
T. aureoviride	8				10			
T. polysporum		10	10		10	10		
Ulocladium sp.			10					
Sterile light-colored mycelium			10			10	10	25
Sterile dark-colored mycelium	8			9				

Note: 1 through 8 are the serial numbers of root fragments 0.5–1 mm in size. The total root length was 12–15 cm.

* The first root fragment (the root tip) was not colonized by fungi in 6 out of 10 cases.

barley hybrid 19304. The reverse was observed with the fungal genera *Trichoderma* and *Acremonium*.

The data on the spatial distribution of micromycetes in the tomato and cucumber rhizoplanes presented in Tables 2 and 3 show that the species diversity of micromycetes was minimal in the apical zone of the roots: on the average, only 6–7 of every 10 roots of these plants were found to be populated in their apical zone with micromycetes of the order *Mucorales*, the genus *Fusarium*, and with an unidentified light-colored sterile mycelium.

The root zone between the zones of root elongation and root hairs was dominated by micromycetes of the order *Mucorales* and the genus *Fusarium* (*F. oxysporum, F. nivale*, and *F. moniliforme*) and, to a lesser degree, by *A. niger, T. harzianum*, and the light-colored sterile mycelium. Microscopic fungi became more diverse in the zone of root hairs (root regions 4, 5, and 6), where the representatives of the genera *Trichoderma (T. hamatum, T. koningii, T. polysporum*, and *T. aureoviride*), *Penicillium* (*P. purpurogenum, P. decumbens*, and *P. melenii*), *Aspergillus* (*A. fumigatus* and *A. niger*), and *Paecylomyces* were detected. This zone was dominated by micromycetes of the order *Mucorales*, the genera *Trichoderma* and *Fusarium*, and, to a lesser degree, by *Acremonium* and *Ulocladium* (in the cucumber rhizoplane) and *Chaetomium* (in the tomato rhizoplane). In this root zone, the fungi of the order *Mucorales* were less abundant than in the apical zone.

In the basal part of the roots, the micromycetes of the genera *Trichoderma, Penicillium* (*P. funiculosum, P. purpurogenum*, and *P. variable*), and *Chaetomium* (in the cucumber rhizoplane) became more abundant. The abundance of the genus *Fusarium* in this zone remained high. The micromycetes of the genera *Gliocladium, Cladosporium* (*C. herbarum*), and *Alternaria* (*A. alternata*) and the sterile dark-colored mycelium were detected only in this zone of the rhizoplane. In the course of the vegetation period of tomato and cucumber plants, the species diversity of fungi colonizing their rhizoplanes somewhat increased (Tables 4 and 5).

Table 3. The spatial distribution of microscopic fungi over the roots of 2-week-old cucumber plants

Fungal taxon	Fungal abundance, %							
	basal root zone			middle root zone			apical root zone	
	8	7	6	5	4	3	2	1*
Acremonium sp.					10			
Aspergillus fumigatus			10			9		
A. niger			10		20	9	20	
Chaetomium sp.		10	10					
Gliocladium fimbriatum			10					
Fusarium oxysporum		10	10	8	10	9	10	
F. solani		10	10		10			
F. moniliforme				8				
Fusarium nivale						9		
Order *Mucorales*	15	10	10	17	10	18	40	66
Paecilomyces sp.				8				
Penicillium canescens	8							
P. melenii				8				
P. purpurogenum	15	30		9				
Penicillium sp.					10			
Trichoderma harzianum	39		10	25	10	9		
T. koningi		10				9		
T. polysporum		10	10	17	10	9		
Ulocladium sp.					10			
Verticillium lateritum			10					
Mycelia sterilia (fam. *Mucedinaceae*)						18	30	33
Mycelia sterilia (fam. *Dematiaceae*)	23	10		8				

Note: 1 through 8 are the serial numbers of root fragments 0.5–1 mm in size. The total root length was 12–15 cm.

* The first root fragment (the root tip) was not colonized by fungi in 7 out of 10 cases.

The spatial distribution of micromycetes in the rhizoplane of 1- to 2-week-old barley plants was similar to that in the tomato and cucumber rhizoplanes (Table 6). Analysis with the use of Hutchinson agar revealed a 2- to 3-fold increase in the species diversity of micromycetes colonizing the basal and middle parts of the roots as compared to their apical zone. It should be noted that we failed to reveal any growth of micromycetes on the Hutchinson agar inoculated with fragments of the root tip and the root elongation zone.

The statistical analysis of the results obtained in this study showed that, irrespective of the plant age, the root zonal differences in the species composition of the micromycete complexes of the tomato and cucumber rhizoplanes are statistically significant with $P < 0.001$ (Table 7). On the other hand, the micromycete complexes of the same rhizoplane zones of the tomato and cucumber plants grown in the same soil did not significantly differ.

The calculated Shannon diversity indices and the Sörensen similarity coefficients confirmed the revealed zonal changes in the species diversity of micromycetes along the root axis (Figs. 1, 2). The species diversity was minimal in the root tip zone of the tomato and cucumber rhizoplanes (the Shannon diversity index = 1.0), whereas this index reached 1.8–2.0 in the root elongation zone and was maximal (2.5–3.1) in the zone of root hairs and in the basal part of the roots (Fig. 1). According to the calculated Sörensen similarity coefficients (68–74%), the micromycete complexes of the root tip and the zone of root elongation are very similar (Fig. 2). At the same time, these micromycete complexes substantially differ from the micromycete complexes of the zone of root hairs (the Sörensen similarity coefficient = 50–60%), the basal part of roots (the Sörensen coefficient = 40–50%), and the upper region of this part (the Sörensen coefficient = 40%).

DISCUSSION

In studies of the spatial distribution of micromycetes over plant roots, more accurate results can be

Table 4. The spatial distribution of microscopic fungi in the tomato rhizoplane at different vegetation stages

First stage (onset of flowering)

Fungal taxon	Fungal abundance, %							
	basal root zone		middle root zone				apical root zone	
	8	7	6	5	4	3	2	1*
Aspergillus niger						20	10	
Alternaria alternata			10					
Chaetomium sp.					10			
Cladosporium herbarum		10						
Fusarium sp.	25		10	10	20	10	40	10
Order *Mucorales*	25	10		10	20	10	40	20
Paecilomvces sp.				10				
Penicillium sp.	25	30	20	30	10	10		
Trichoderma hamatum	25	40	30	30	40	40		
Ulocladium sp.			10					
Sterile light-colored mycelium			10			10	10	10
Sterile dark-colored mycelium				10				

Second stage (flowering)

Fungal taxon	Fungal abundance, %							
	basal root zone		middle root zone				apical root zone	
	8	7	6	5	4	3	2	1*
Aspergillus niger			10			17		
Alternaria alternata			10					
Chaetomium sp.	8							
Cladosporium herbarum	8				10			
Fusarium sp.	31	17		10	20		8	
Order *Mucorales*	8	33	10	40	30	17	50	10
Paecilomvces sp.			10					
Penicillium sp.	23	17	20	20	20	17		
Trichoderma hamatum	15	17	40		20	33	25	
Vertisillium lateritum				10				
Sterile light-colored mycelium						17	17	
Sterile dark-colored mycelium	8	17		20				

Third stage (maturation)

Fungal taxon	Fungal abundance, %							
	basal root zone		middle root zone				apical root zone	
	8	7	6	5	4	3	2	1*
Aspergillus niger	7	12	8	7	7			10
Alternaria alternata					14			
Chaetomium sp.				7	14			
Gliocladium sp.	7					8		
Fusarium sp.	20	18	15	7	7	17	15	10
Order *Mucorales*	30	31	15	20	14	42	58	10
Penicillium sp.		13	20	20	21	8	7	
Trichoderma hamatum	20	12	42	25	25	16	7	
Sterile light-colored mycelium		6		7		8	7	
Sterile dark-colored mycelium	15	6		7				

Table 5. The spatial distribution of microscopic fungi in the cucumber rhizoplane at different vegetation stages

First stage (onset of flowering)

Fungal taxon	Fungal abundance, %							
	basal root zone		middle root zone				apical root zone	
	8	7	6	5	4	3	2	1*
Aspergillus niger						20	10	
Alternaria alternata			10					
Chaetomium sp.					10			
Cladosporium herbarum		10						
Fusarium sp.	25		10	10	20	10	40	10
Order *Mucorales*	25	10		10	20	10	40	20
Paecilomyces sp.				10				
Penicillium sp.	25	30	20	30	10	10		
Trichoderma hamatum	25	40	30	30	40	40		
Ulocladium sp.			10					
Sterile light-colored mycelium			10			10	10	10
Sterile dark-colored mycelium				10				

Second stage (flowering)

Fungal taxon	Fungal abundance, %							
	basal root zone		middle root zone				apical root zone	
	8	7	6	5	4	3	2	1*
Aspergillus niger			10			17		
Alternaria alternata			10					
Chaetomium sp.	8							
Cladosporium herbarum	8				10			
Fusarium sp.	31	17		10	20		8	
Order *Mucorales*	8	33	10	40	30	17	50	10
Paecilomyces sp.			10					
Penicillium sp.	23	17	20	20	20	17		
Trichoderma hamatum	15	17	40		20	33	25	
Verticillium lateritum				10				
Sterile light-colored mycelium						17	17	
Sterile dark-colored mycelium	8	17		20				

Third stage (maturation)

Fungal taxon	Fungal abundance, %							
	basal root zone		middle root zone				apical root zone	
	8	7	6	5	4	3	2	1*
Aspergillus niger	7	12	8	7	7			10
Alternaria alternata					14			
Chaetomium sp.				7	14			
Gliocladium sp.	7					8		
Fusarium sp.	20	18	15	7	7	17	15	10
Order *Mucorales*	30	31	15	20	14	42	58	10
Penicillium sp.		13	20	20	21	8	7	
Trichoderma hamatum	20	12	42	25	25	16	7	
Sterile light-colored mycelium		6		7		8	7	
Sterile dark-colored mycelium	15	6		7				

Table 6. The spatial distribution of microscopic fungi in the rhizoplane of 2-week-old barley (hybrid 19304) plants

Fungal taxon	Fungal abundance, %													
	basal root zone				middle root zone						apical root zone			
	7		6		5		4		3		2		1	
	1*	2**	1	2	1	2	1	2	1	2	1	2	1	2
Acremonium sp.				13		5					9		17	
Aspergillus niger		5												
Alternaria alternata						5								
Humicola grisea		46				5								
Fusarium sp.	26	27		45	9	25		35		15		17		
Order *Mucorales*	47	14	80	25	65	30	75	50	75	55	73	75	75	80
Family *Piptocephalidaceae*		4								5				10
Penicillium sp.	27		15	6	26	10	25	5	25	5	18	8		
Scopulariopsis sp.										15				
Stysanus stemonitus		4	5	6						5				
Zygorhynchus sp.								5					8	10
Mycelia sterilia				5		20	5	5						

Note: 1 through 7 are the serial numbers of root fragments 0.5–1 mm in size. The first root fragment (the root tip) was not colonized by fungi in 5 out of 15 cases. The total root length was 12–15 cm.

* 1, fungal population was analyzed with Czapek agar. ** 2, fungal population was analyzed with Hutchinson agar.

obtained if test media are inoculated with root fragments instead of root washings. If it is difficult to mechanically clean the roots from soil particles, the experimental plants can be grown in such a way that their roots appear between the two layers of a small-mesh-size gauze. This allows one to obtain a plant rhizoplane not contaminated with soil particles.

Analysis of the species abundance of micromycetes in the apical zone of the roots showed that it corresponds (with $p > 0.05$) to the model of geometrical series (Fig. 3b), which is typical of the early succession stages of microbial communities when their species occupy the free space in the niche within equal time periods [12]. At the same time, the species abundance of micromycetes in the basal root zone and in the zone of root hairs corresponds (with $p > 0.05$) to the model of log series (Figs. 3c, 3d), which describes microbial communities composed mainly of rare species and distinguishable by a small number of dominant species and random time intervals at which the species occupy free space in the niche. The species abundance of micromycetes in the rhizoplane of 2-week-old tomato plants corresponded to the log series model (Fig. 3a) and, in the rhizoplane of mature tomatoes, to the log–normal model, which describes developed microbial communities with diverse species [13]. The species abundance of micromycetes in the cucumber rhizoplane was similar. It should be noted that species abundance in the micromycete complex of soddy podzolic soils can be adequately described by the model of Macarthur's broken rod and log–normal series [13].

The data available in the literature on the fungal population of the root tip are very limited and contradictory. For instance, Sulochana found that the cotton root tip was colonized by micromycetes [14], whereas Parkinson presented opposite data [15].

Our studies showed that the root tip is seldom, if at all, colonized by micromycetes. This finding was confirmed both by scanning electron microscopic observations [6] and by the direct inoculation of Czapek and Hutchinson agars with root fragments (the latter exper-

Table 7. Evaluation of the effect of various factors (root zone, plant species, and plant age) on the species structure of micromycete communities

Factor	Degree of influence*	Significance level
Cucumber root zone	0.16	$P < 0.001$
Tomato root zone	0.19	$P < 0.001$
Root zone of both plants	0.28	$P < 0.001$
Plant age	0.41	$P < 0.001$
Plant	0.92	$P < 0.332$

* The degree of influence was calculated as the ratio of the determinant of the intergroup covariant matrix to the determinant of the general covariant matrix (Wilk's λ).

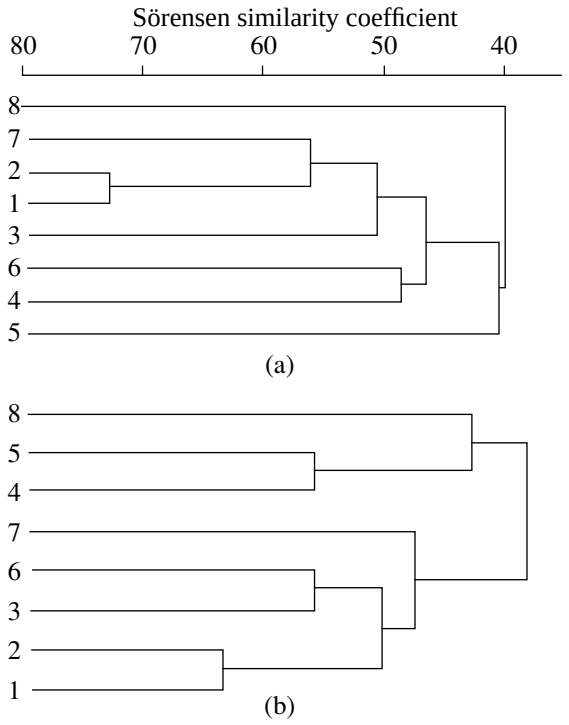

Fig. 1. Similarity of the micromycete complexes colonizing the different zones of the rhizoplane of (a) tomato and (b) cucumber plants: 1, 2, and 3, the basal part of roots; 4, 5, and 6, the zone of root hairs; 7, the root elongation zone; and 8, the root tip.

iments showed the absence of micromycetes on the root tip in 60–100% of the cases). This fact can be explained by root elongation at a rate that exceeds the mean linear growth rate of soil bacteria and fungi, so that they do not have time to propagate from the colonized portions of the root to its newly growing uncolonized portions. Alternatively, microbial colonization of the root tip may be prevented by the secretion of antibiotic substances by this part of the root. With plant maturation, both the occurrence and abundance of micromycetes in the apical root zone increase, which can be accounted for by the slowing down of the root growth and a diminishing amount of secreted antibiotic substances.

The micromycetes colonizing the root tip and the zone of root elongation were dominated by fast-growing (with a linear growth rate of 0.7–1.2 mm/h) *R* strategists (*Mucorales*, *Mycelia sterilia*, and *F. oxysporum*). According to the data of Sulochana, related fungi, *F. solani* and *Rhyzopus oryzae*, colonize the cotton root tip [14]. The root elongation zone and the region bordering the root hair zone were mainly colonized by fusaria, *A. niger*, and, to a lesser degree, by *Trichoderma*. The zone of root hairs and the basal root portion were colonized by fungi of the genera *Penicillium*, *Alternaria*, *Gliocladium*, *Chaetomium*, *Paecilomyces*, *Ulocladium*, *Trichoderma*, *Talaromyces*, and some others, many of which are typical cellulolytics. After the inoculation of Hutchinson agar with root fragments of these zones, fungal colonies began to grow in later terms, appeared in a lower number, and grew slower than after the inoculation of this agar with fragments of the root tip and elongation zone. Therefore, unlike the microbial population of the apical root zone, which is mainly represented by the fast-growing *R* strategists, the microbial population of the middle and basal portions of roots is mainly represented by slow-growing *K* strategists. Similar changes in the microbial population of the rhizoplane were observed in relation to plant development [16].

The fungal population of different root portions is governed by the amount and composition of root exudates, the amount of dying root cells, the rate of elongation of different root zones, and other reasons. The colonization of the root as a whole and its particular zones is species-specific. For instance, the cucumber rhizoplane is mainly populated by the fungal species *T. harzianum*, whereas the tomato rhizoplane, by *T. hamatum*. The population of *F. oxysporum* is maximal in the root zone nearest to the root tip. Similarly, the population of *Verticillium dahliae* and *F. oxysporum* was found to be maximal at a distance of 1–2 cm from the cotton root tip [5].

The colonization of the tomato and cucumber rhizoplanes by fusaria earlier than by micromycetes of the genera *Trichoderma*, *Gliocladium*, *Penicillium*, and others may explain the failure of the attempts to control root diseases through the introduction of *Trichoderma* and *Gliocladium* species [16]. Indeed, even though an introduced antagonistic strain is able to colonize a root, virulent *Fusarium* races can colonize it in earlier terms, thus preventing the colonization of the root by the introduced strain. The data presented here show that, to be efficient against particular root infections, introduced antagonistic strains must be able to rapidly colonize the rhizoplane. Good candidates for this are the fast-growing fungi forming the light-colored sterile mycelium and the fungi of the order *Mucorales*. In the case of the barley hybrid 18505, the fungi of the genus *Acremonium* also holds considerable promise. *Mucorales*, which are typical *R* strategists, show rapid germination and growth, produce massive mycelium, and are able to colonize the fast-growing portions of the root, including the root tip. However, they have some disadvantages, such as weak interpopulation interactions and inability to form antibiotic substances [10]. As a result, in the zone of root hairs and in the basal portion of the root, where the population of other fungi is dense, the population of mucorales is diminished. The possibility, however, cannot be excluded that new strains of mucorales can be found or obtained by genetic engineering methods, which will be more competitive with respect to phytopathogenic microorganisms.

Recently, a new approach to control root pathogens has been proposed, which lies in the introduction of

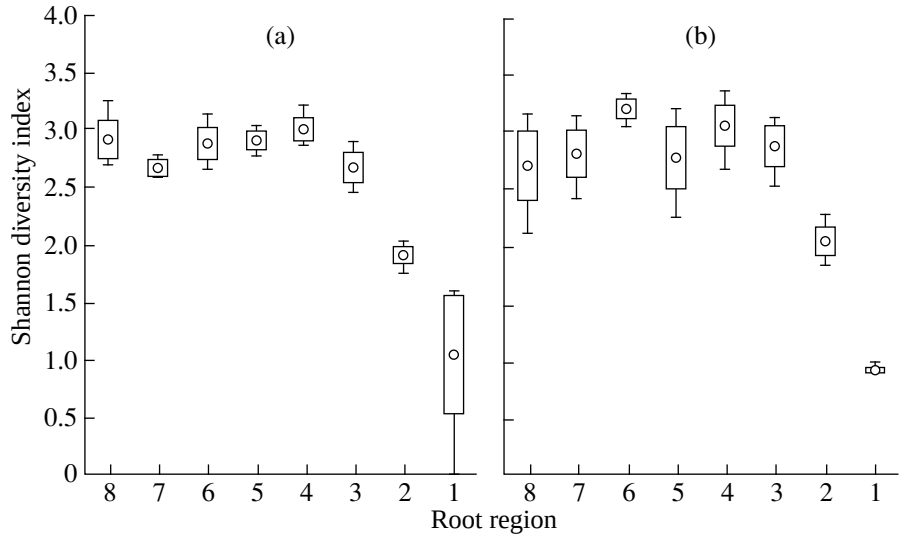

Fig. 2. The species diversity of the microscopic fungi colonizing the different zones of the rhizoplane of (a) tomato and (b) cucumber plants: 1, 2, and 3, the basal part of roots; 4, 5, and 6, the zone of root hairs; 7, the root elongation zone; and 8, the root tip.

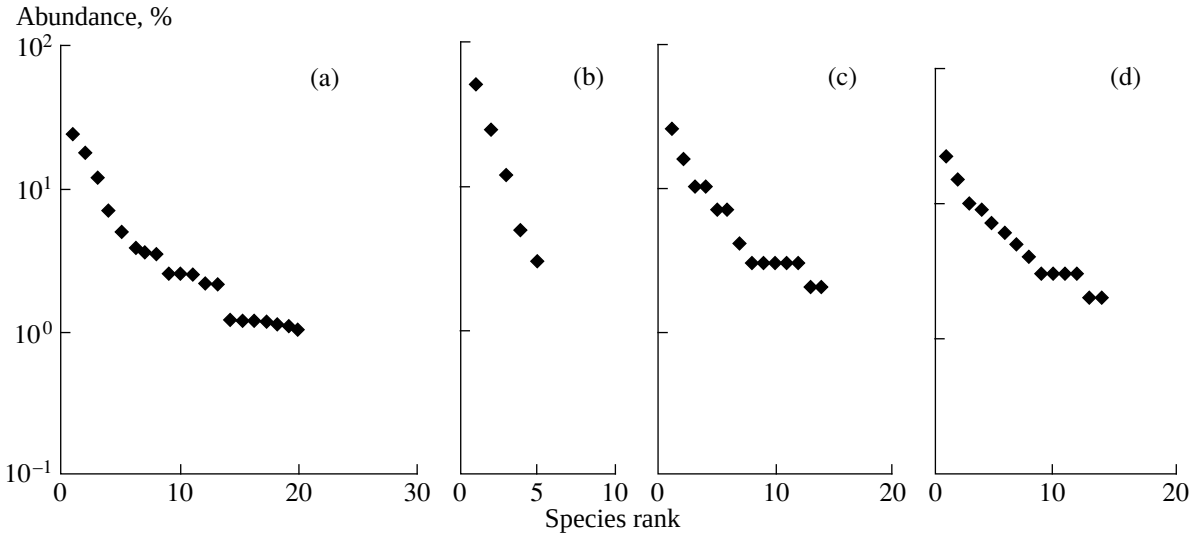

Fig. 3. The distribution curves of the species abundance of microscopic fungi in (a) the rhizoplane of 2-week-old tomato plants and in (b) the apical zone, (c) the root hair zone, and (d) the basal zone of their roots.

nonpathogenic allied strains to the rhizoplane [18]. For instance, the preliminary inoculation of the sweet potato rhizoplane with the nonpathogenic *F. oxysporum* sp. prevented their colonization with the pathogenic *F. oxysporum* f. sp. *batatas* [19], and the introduction of the saprotrophic fungus *Fusarium* sp. to soil led to its resistance to fusarium wilt [20]. These results can be explained by the induction of defense reactions in host plants by nonpathogenic strains or by the competition between pathogenic and nonpathogenic strains for common nutrients [21].

Saprotrophic fusaria (*F. oxysporum* and other species) are the first to colonize the rhizoplane. This implies that nonpathogenic fusarial strains must efficiently compete with phytopathogenic bacterial strains for common econiches in the rhizoplane and, hence, may prevent the phytopathogen invasion of plants.

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